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PREDATOR AVOIDANCE BEHAVIORS OF FIVE SPECIES OF PANAMANIAN ORB-WEAVING SPIDERS (ARANEAE; ARANEIDAE, ULOBORIDAE)

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ABSTRACT

The responses of five tropical orb-weaving spiders (family Araneidae and Uloboridae) to predatory attacks by salticids and hummingbirds were observed. Responses varied between species and predators. Salticid attacks dorsal to orb-weavers on the web evoked rapid movements which displaced the salticid from the orb-weaver's dorsum. Ventral salticid attacks were countered by stilting. Attacks by hummingbirds evoked dropping or retreat from the web surface. *Uloborus republicanus* (Simon) without eggmasses dropped more frequently than *U. republicanus* with eggmasses when attacked by hummingbirds. *Cyclosa caroli* (Hentz) did not respond to hummingbird attacks directed toward the debris-like stabilimentum; however, salticid spider contacts on the *Cyclosa* or stabilimentum evoked active defense.

INTRODUCTION

Tolbert (1975) described the predator avoidance behaviors of the orb-weaving spiders *Argiope aurantia* (Lucas) and *Argiope trifasciata* (Fôrskal) using an artificial model. The use of models as stimuli to elicit behavioral responses has obvious drawbacks when the sign stimuli or recognition patterns are not known. Nevertheless, Tolbert (1975) provided an important first look at predator avoidance patterns in araneids.

This study examines the predator avoidance patterns of four species of tropical araneids and one uloborid. Two types of predators were examined; ambulatory and aerial predators.

METHODS

Four species of araneid and one uloborid were used as prey in staged predatory interactions involving salticid (Araneae) and hummingbird (Trochilidae) predators. The prey spiders were collected from second growth areas along Pipeline Road, near Gamboa, Panamá. Spiders were returned to Barro Colorado Island, Panamá, measured, and released into one of two adjoining 3 x 3 x 2 m insectary rooms. A fruit fly culture (*Drosophila* sp.) was maintained in each insectary room to provide food for the spiders.

The response of orb-weaving spiders to salticid predation was studied using the large salticid *Phiale guttata* (C. L. Koch), captured from the Pipeline Road collecting sites. Salticids were maintained in 3 x 10 mm plastic vials, corked with foam rubber. Salticids

were watered daily but fed infrequently to maintain their responsiveness to prey (Gardner 1964). Predatory encounters were staged by placing a slaticid on a 1.5 cm wooden platform which was held 3-5 cm from the intended prey. This method is consistent with records of salticid-araneid encounters (Robinson and Valerio 1977). The species of the intended prey was recorded, along with the point at which the salticid contacted the web or intended prey, the response of the intended prey, and the outcome of the encounter.

The response of orb-weaving spiders to hummingbird predation was studied using the hermit hummingbird, *Phaethornis superciliosus* (Linné). Hummingbirds were mistnetted on Barro Colorado Island, Panamá, placed in an insectary, and fed a 20% sugar solution without protein for two days prior to release into the insectaries containing spiders.

All observations were made from within the insectaries. In all cases, my presence had little effect upon the activities of the predator or prey. A three-way test of independence (G test, Sokal and Rohlf 1969) was used to examine the independence of predator (hummingbird or salticid), prey species, and behavior. A Fisher exact test (Sokal and Rohlf 1969) was used to examine the differential response of uloborids with and without an eggmass.

RESULTS AND DISCUSSION

The three way interaction of prey species, predator species, and behavior is statistically significant (G test, $P < 0.01$). This indicates that predator avoidance behaviors vary, depending upon the species of araneid or uloborid attacked, and the predator. The apparent selection of different prey by hummingbirds and salticids may be an artifact of the experimental design, since salticids were not allowed to forage freely, nor were they offered the entire range of prey.

***Phiale guttata* (C. L. Koch) (Family Salticidae).**—The results of staged salticid-araneid interactions are presented in Table 1. Because of the artificial nature of the experiment, it is difficult to determine whether all salticid jumps were the result of predator attacks. Since the presentation of unoccupied platforms did not affect the behavior of the intended prey, I assume that the behavioral responses to salticid jumps reflect normal predator avoidance patterns, rather than abnormalities induced by the experimental method.

Three attacks involving immature *Nephila clavipes* (Linné) resulted in kills. In each case the salticid jumped onto the *Nephila*'s abdomen and bit the *Nephila* immediately behind the cephalothorax. The salticid carried the prey to the platform via a dragline secured prior to the attack, and consumed the prey.

The position of the salticid's impact with the web or araneid has a strong effect (G test $P < 0.5$) on the responses of *Argiope argentata* (Frabricius) and *Nephila clavipes* (Table 1). Prey capture behaviors occurred in 72% of the instances when the salticid contacted the catching spiral of the web (n = 36, Table 1). In *A. argentata*, rapid lateral movements comprised 68% of the response to dorsal body contact (n = 29, Table 1). Pumping occurred in 16% of ventral contacts and 16% of catching spiral contacts. In *N. clavipes*, rapid lateral movements accounted for 100% of the response to dorsal body contact. Pumping occurred only once, in response to contact on the catching spiral (n = 11, Table 1). In both *A. argentata* and *N. clavipes*, stilting occurred only in response to ventral hub contacts.

Responses of the cryptic species, *Cyclosa caroli* (Hentz) to contact by salticids are presented in Table 1. Pumping and lateral movements comprised 75% of the response to

Table 1.–The responses of orb-weaving spiders to predation by the jumping spider *Phiale guttata*. Unless otherwise indicated, all orb-weaving spiders were adult females. D = dorsal presentation; V = ventral presentation; CS = catching spiral.

Species		Behaviors						
		No Response	Prey Capture	Pump	Rear	Stilt	Move	Drop
Argiope argentata	D	2	1		3		19	2
	V	3		2	1	5		1
	CS	2	15	4		3		
Nephila clavipes	D						11	
	V					7	3	1
	CS		11	1				
Cyclosa caroli			2	6			6	2
Uloborus republicanus		2		1			9	1

salticid contact on the araneid or the debris-like stabilimentum (n = 16). Attacks and drops were equally common, accounting for the remaining 25% of the response.

The spider *Uloborus republicanus* (Simon) keeps the eggmass in the web, attached to the spider by a dragline issuing from the spinnerets. Rapid lateral movement was the most common response (69%) to salticid contacts. Uloborids with eggmasses carried the eggmass, attached to the spinnerets, away from the predator when moving. Uloborids with eggmasses did not drop, an act which would require abandoning the eggmass. Uloborids without eggmasses dropped 20% of the time (n = 13). No response was a component of the defense of uloborids with eggmasses only. This trend was not significant (Fisher exact test, P = 0.35).

The prevalence of stilting in response to ventral attacks involving *Argiope argentata* correlates with Tolbert's (1975) report of predator avoidance in *A. aurantia* and *A. trifasciata*. The incidence of prey capture behaviors in response to salticid contact on the catching spiral probably relfects a predatory, rather than defensive, response (Robinson and Robinson 1973, Robinson and Olazarri 1971). Rapid lateral movements, switching, etc., dislodge the salticid before it can bite the prey. Dropping, seen infrequently in Tolbert's (1975) study, was a component of salticid contacts on or near the orb-weaver itself. Dropping is common in the field, often occurring upon the observer's approach. Dropping removes the spider from the web, a visual stimulus for aerial predators (Edmunds 1974); however, dropping may bring the spider into contact with predators on the vegetation.

***Phaethornis superciliosus* (Linné) (Family Trochilidae).**–Hermit hummingbirds are known to forage on orb-weaving spiders (Young 1971). Foraging is characterized by low flights and examination of the web area. Attacks are usually dorsal, directed toward small spiders (body length < 7 mm), kleptoparasites, eggmasses and insects in the web.

Forty percent of all attacks results in prey captures; however, in 60% of the attacks (n = 152), the hummingbird did not capture a spider in its first lunge. These instances were used to examine the spider's antipredator behaviors. *Uloborus republicanus* and second instar *Nephila clavipes* (body length < 7 mm) dropped in response to hummingbird attacks 61 and 62% of the time (n = 90, Table 2). *Leucauge venustra* (Walckenaer) moved (25%), dropped (16%), or did not respond (42%) to hummingbird attacks (n = 12, Table 2). Adult *N. clavipes* pumped (49%), dropped (7%), stilted (7%), reared (7%), or did not respond (28%) to hummingbird attacks (n = 14, Table 2).

Table 2.–The responses of orb-weaving spiders to predation by the hummingbird *Phaethornis superciliosus*. Unless otherwise indicated, all spiders were adult females. (2) = second instar spider, sex unknown; (E) = eggmass in the web.

	Behaviors						
Species	No Response	Prey Capture	Pump	Rear	Stilt	Move	Drop
Argiope argentata			2		5	2	
Cyclosa caroli	5	1	1				
Leucauge venustra	5		2			3	2
Nephila clavipes	4		7	1	1		1
Nephila clavipes (2)	4		6		3		20
Uloborus republicanus	18						33
Uloborus republicanus (E)	5						1

Pumping second instar *Nephila clavipes* were eaten readily, 80% of the time. Dropping and retreat afforded the best survival for small spiders (body length < 7 mm). Adult *Leucauge venustra, Argiope argentata* and *N. clavipes* survival was 100% regardless of behavior. This is apparently related to the large size of these spiders relative to the prey size range preferred by *Phaethornis*.

Cyclosa caroli did not respond to 86% of the hummingbird attacks directed toward the debris-like stabilimentum (n = 7). This pattern is highly adaptive and characteristic of cryptic animals (Edmunds 1974, Robinson 1969). One out of three attacks involving *C. caroli* without debris was immediately successful. No attacks involving *C. caroli* with complete debris stabilimentum were successful and none was oriented toward the spider (n = 3); however, one attack to the *Cyclosa* with an incomplete stabilimentum (no debris below the spider) was successful.

The differential response between *Uloborus republicanus* with and without eggmasses is of particular interest. *Uloborus republicanus* without eggmasses dropped in response to hummingbird predatory attacks. *Uloborus republicanus* with eggmasses did not respond to hummingbird attacks (Fisher exact test, $P < 0.05$). This differential response indicates that predator avoidance behaviors are modified to reflect the cost of capture. Dropping may not be adaptive for *U. republicanus* with an eggmass because movement attracts the hummingbird to the web. Once attracted to the web, there is a high probability that the hummingbird would eat the abandoned eggmass.

The sequential production of eggmasses in *Uloborus republicanus* may involve a decreasing fecundity or viability per eggmass, or, the energetic investment per eggmass may be sufficiently high to warrant eggmass protection (Anderson 1978). Nonetheless, it is adaptive for an individual uloborid to protect its investment in the eggmass. The lack of response to hummingbird attacks provides eggmass protection.

CONCLUSION

Dropping was most frequently employed by small spiders against hummingbirds. Dropping provides a rapid escape and protection by substrate vegetation. After dropping, the spider can return to the hub of the web via its dragline. Pumping was not an effective deterrent to hummingbird predation.

Rapid lateral movements were the most frequent response to dorsal salticid attacks, Such movements tended to dislodge the salticid and throw it into the catching spiral where it was attacked. Pumping, used less frequently in response to salticid predation, also resulted in displacement of the salticid. Ventral attacks were countered by stilting or rapid lateral movements. Stilting interposes the hub between the salticid and the orb-weaver and frequently prevents successful captures.

Data from hummingbird-uloborid encounters indicate that the behavioral response to predation can be modified by spiders with and without eggmasses. This variation is adaptive; by modifying the behavioral response to predation, the spider can protect its investment in the eggmass.

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